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# Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA

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**Abstract.** Within the last century there has been widespread establishment of trees in mountain meadows of the Pacific Northwest. We reconstructed patterns of tree invasion at 17 meadow sites in the central Cascade Range of Oregon, USA – sites representing diverse physical environments and vegetation types and experiencing different histories of recent anthropogenic disturbance (sheep grazing). Spatial distributions and age structures of invasive tree populations were analysed with respect to climatic records and grazing history. Patterns of establishment varied considerably among meadows, reflecting strong differences in environment and grazing history. In montane hydric meadows, tree establishment was spatially clumped beneath large old trees and on elevated microsites; however the timing of invasion differed between sites with stable versus fluctuating water tables. In upland mesic/dry montane meadows, timing of invasion corresponded with cessation of sheep grazing (early 1940s) and the onset of wetter summers (mid 1940s). In the subalpine zone, climate and aspect interacted to produce contrasting histories of invasion on north- and south-facing slopes.

Establishment on north-facing slopes, concentrated in heath-shrub communities, coincided with regional warming (ca. 1920-1945) when snowpacks were lighter and melted earlier. Recruitment of trees onto south-facing slopes occurred later, when conditions were wetter (1945-1985). In many environments, the spatial distribution of recruitment suggests that once trees have established, autogenic factors become increasingly important as individual trees or groups of trees alter the physical or biotic conditions that once inhibited establishment.

Knowledge of the factors that influence invasion, and of their varying importance across gradients in environment and vegetation, is critical to predicting future changes in these dynamic systems.

**Keywords:** Climate change; Ecotone; Forest-meadow boundary; Meadow invasion; Montane meadow; Pacific Northwest; Subalpine meadow; Three Sisters Biosphere Reserve; Tree ring.

**Abbreviations:** TSBR = Three Sisters Biosphere Reserve/ Wilderness Area.

**Nomenclature:** Hitchcock & Cronquist (1973).

## Introduction

Meadows are conspicuous and dynamic features of the forested mountain landscapes of the western United States. In the mountains of the Pacific Northwest, meadows occupy various elevations and topographic positions: montane ridge-tops, south-facing hill-slopes, basins, valleys and other poorly drained topography, and the vast parkland of the subalpine zone (Franklin & Dyrness 1988). The origin and persistence of meadows in areas that can ostensibly support dense, coniferous forest have been the subject of widespread investigation (e.g. Kuramoto & Bliss 1970; Franklin et al. 1971; Vale 1981; Magee & Antos 1992; Rochefort et al. 1994; Woodward et al. 1995; Rochefort & Peterson 1996). Palaeo-ecological evidence (e.g. Wood 1975; reviews in Rochefort et al. 1994) and recent observations of widespread invasion of meadows by trees suggest that meadows are not stable features of the landscape. Rather, the boundaries between forest and meadow can be dynamic over relatively short or long intervals of time.

Many factors, both physical and biotic, have been related to episodes of tree establishment or to periods of meadow stasis. These include: (1) changes in temperature and/or precipitation that result in longer growing seasons or, conversely, more stressful microclimatic conditions (Brink 1959; Fonda & Bliss 1969; Franklin et al. 1971; Butler 1986; Taylor 1995; Woodward et al. 1995; Rochefort & Peterson 1996); (2) the effects of grazers or wildfires that may either consume seedlings or create open sites for establishment (Dunwiddie 1977; Vankat & Major 1978; DeBenedetti & Parsons 1979; Vale 1981; Ratliff 1985; Vallentine 1990); or (3) autogenic factors that reduce the inhibitory effects of ground-layer communities (e.g. Magee & Antos 1992). To a large degree, however, these relationships have been examined within a narrow ecological context: studies have been conducted in individual meadows or in small groups of meadows with similar characteristics (but see Woodward et al. 1995; Rochefort & Peterson 1996). Consequently, it is unclear how these mechanisms vary in importance across multiple gradients of environment (e.g. elevation, topography, hydrology), disturbance, or vegetation. Our ability to predict future changes in the composition and distribution of forest and meadow vegetation at larger spatial scales requires an understanding of how these factors interact or vary in time and space. In this study, we reconstruct the temporal and spatial patterns of tree invasion at 17 sites in the Three Sisters Wilderness Area/Biosphere Reserve (central Cascade Range, Oregon, USA) – sites that span broad gradients in physical environment (montane to subalpine zones, hydric to xeric soils), vegetation (graminoid-, herb-, and shrub-dominated meadows), and disturbance (minimal to intensive grazing by sheep). We provide evidence to illustrate that multiple factors – both allogenic and autogenic – shape patterns of tree invasion, and that the strengths of these effects vary or interact in space and time, producing a complexity of pattern that may not be discernible at smaller spatial scales.

## Methods

### *The study area*

#### *Physical environment*

The Three Sisters Wilderness Area/Biosphere Reserve, henceforth TSBR, encompasses nearly 100 000 ha of relatively undisturbed, mountainous landscape straddling the central Cascade Range of Oregon, USA (Fig. 1; Franklin 1979). Two physiographic provinces are represented: the Western Cascades and the High Cascades (Franklin & Dyrness 1988). The Western Cascades are more deeply dissected, composed of older volcanic flows and pyroclastic deposits of Oligocene and Miocene origin (Orr et al. 1992). Primary ridge crests average 1500 m a.s.l. and few peaks exceed 1800 m a.s.l. Soils vary in their physical properties but most are derived from basalts, andesites, and pyroclastics (primarily tuffs and breccias) (Franklin & Dyrness 1988). The High Cascades which lie to the east of this range are geologically younger, composed of Quaternary shield and composite volcanoes. The topography is more gentle and rolling, sloping upward toward the primary peaks in the Wilderness – North, Middle, and South Sister, contiguous stratovolcanoes > 3000 m a.s.l. (Fig. 1). Soils in the High Cascade Province are deep and well drained, composed of recent deposits of pumice, ash, and cinders.

Although the climate varies with elevation and topography, winters are generally mild and wet, and summers, cool and dry. Mean annual precipitation ranges from 800 mm at lower elevations in the rain shadow of the Western Cascades, to 3300 mm at higher elevations; ca. 6 % falls between June and August (Hemstrom et al. 1987; Bierlmaier & McKee 1989). Snow accumulations are deepest in May (often exceeding 4 m in depth above 1 000 m a.s.l.) and some meadow communities may remain buried as late as August (Campbell 1973).

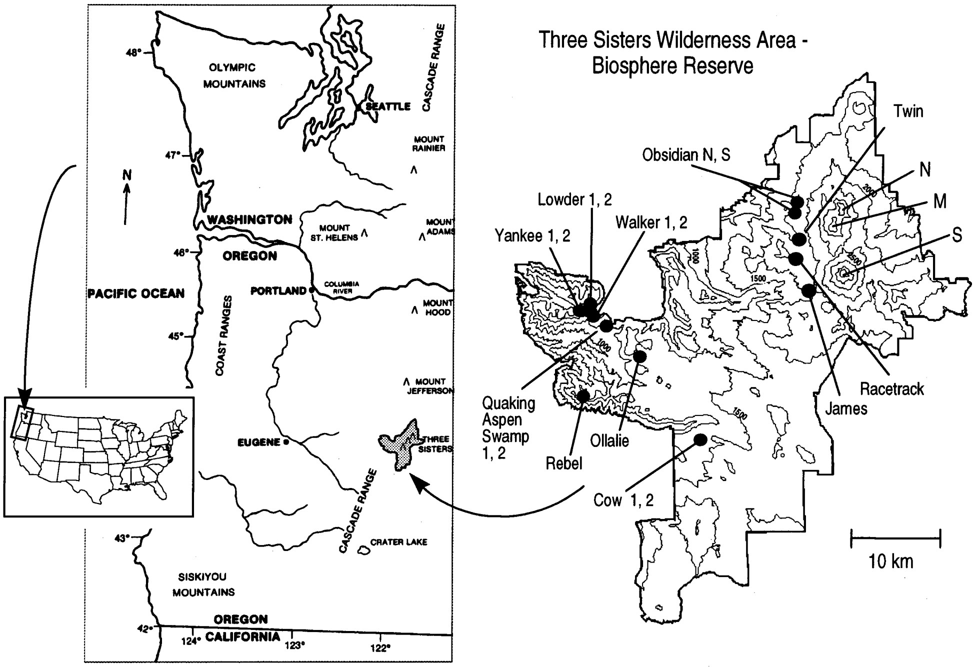

**Fig. 1.** Location of permanent transects in the Three Sisters Wilderness Area / Biosphere Reserve, Oregon. Note the steeper topography in the western Cascades. N, M and S are North, Middle, and South Sisters, respectively.

Temperatures average 8.5 °C annually, 0.6 °C in January, and 17.8 °C in July at the nearby H. J. Andrews Experimental Forest (426 m; Bierlmaier & McKee 1989).

*Vegetation*

In the montane zone (below ca. 1600 m a.s.l.), forests are variously dominated by *Abies grandis*, *Pseudotsuga menziesii*, *A. amabilis* and *Pinus contorta* (Peinado et al. 1997: alliances D1, D2); and meadows are most commonly found on steep south-facing slopes, in small hydric basins, and in areas of flat, but poorly drained topography (Halpern et al. 1984; Hemstrom et al. 1987). Forests of the subalpine zone (ca. 1600 - 2000 m a.s.l.) are dominated by *Tsuga mertensiana*, but *Abies lasiocarpa* and *Pinus albicaulis* are abundant on colder and drier sites (Halpern et al. 1984; Franklin & Dyrness 1988; Peinado et al. 1997: alliance D2). At these higher elevations, meadows and other non-forested communities dominated by graminoids, herbs, or heath-shrubs are interspersed with forests or tree islands, forming extensive mosaics of subalpine parkland. Although subalpine meadows are most common on the gentle slopes and in the broad basins that flank the Three Sisters peaks, they also occur on high ridges and plateaus to the west. Halpern et al. (1984) have classified and described 40 meadow communities and phases for TSBR and adjacent areas.

*Disturbance history*

Historically, the primary agent of natural disturbance in TSBR, as elsewhere in the central Cascade Range, has been wildfire. Although no investigations have been conducted in the Wilderness, studies from adjacent areas suggest a complex history of fire. The regime can be characterized as episodic. During the last five centuries, fires have varied in frequency, intensity, and spatial extent, with return intervals ranging from 95 - 150 yr in the *Tsuga heterophylla* forest zone (i.e. lower elevations in the montane zone) (Teensma 1987; Morrison & Swanson 1990). Although poorly documented, fires in upper montane and subalpine forests are thought to be far less common (Agee 1993). Coarse estimates of stand age obtained during reconnaissance sampling in the Separation Creek drainage, TSBR (Halpern et al. 1984) suggest major fire episodes between 1840 and 1890 at lower elevations with occasional reburns on drier slopes. Stands of ca. 185 - 270 yr occur at higher elevations in the montane zone and old-growth forests (350 - 550+ yr) are primarily found in the subalpine, dominated by *T. mertensiana* or *A. amabilis*.

Although anthropogenic ignitions are known to have been important in maintaining open conditions in lowland valleys of western Oregon (Johannessen et al. 1971), evidence of intentional aboriginal burning of mountain meadows is lacking for the central Cascades (Burke 1979; Teensma 1987). During the post-European settlement period (ca. 1850-1910) human-induced fires are known to have occurred in association with road building, sheep grazing and camping (Burke 1979; Vale 1981). To what extent the frequency, intensity, and spatial extent of these pre- and post-settlement fires deviated from those of the natural fire regime remains unclear. None of our sites exhibited evidence of recent fire (e.g. burned snags or visible logs) although charcoal was occasionally found in soil samples.

Although historical records are scarce, it is likely that sheep grazed meadows in the area of TSBR as early as 1870 (G.W. Williams pers. comm.). The highest densities of sheep occurred between 1880 and 1910 (Minor & Pecor 1977; Rakestraw & Rakestraw 1991; G.W. Williams pers. comm.). Before the Forest Service administered grazing allotments in 1898, unrestricted grazing eroded soils and reduced plant cover in some meadows (Coville 1898; Kuhns 1917; Ingram 1922; Elliot 1946; Rakestraw & Rakestraw 1991). Between 1920 and 1938, many areas were closed to grazing because of deteriorating range quality and increasing conflict with recreational users (Elliot 1946). Sheep last grazed in TSBR in 1947 (Johnson 1985). Grazing by cattle was rare, limited to a small area east of our study sites between 1944 and 1966 (Anon. 1969; F. C. Hall pers. comm.).

*Field methods*

In 1983, as part of a broader study of the composition and dynamics of ecosystems in TSBR, 21 permanently marked transects were established across forest-meadow boundaries at 17 sites (Halpern et al. 1984, 1991). Transect locations were chosen to encompass a range of environments and vegetation types, and to represent a diversity of tree invasion patterns. Of these original transects, 15 were resampled in 1993 at which time one was lengthened and two non-permanent transects were added (Table 1). Transects vary in length from 50 - 150 m and in width from 5 - 30 m (one transect is 2 m wide; Table 1).

At each transect, elevation, slope, aspect, and topography were recorded and a set of soil pits was dug to assess soil texture and for hydric sites, the presence and relative depth of the water table (Table 1). To quantify the ground layer vegetation, the cover of all vascular plant species was visually estimated in a series of 1 m × 1 m plots spaced 1 - 2 m apart on alternating sides of each transect. Trees were sampled in contiguous plots along both sides of each transect; transect width varied by site and by size-class of tree (Table 1). Tree densities were standardized across sites and size-classes by dividing by the areas sampled. Species, height, diameter

**Table 1.** Primary invading tree species, vegetation, site characteristics, and the dimensions of the 17 study transects.

| Transect | Primary invading tree species | Principal plant community[a] | Mean elev. (m) | Aspect | Slope (%) | Meadow soil texture[b] / hydrology[c] | Allotment closure | Transect length/width[d] (m) |
|---|---|---|---|---|---|---|---|---|
| **Montane sites** | | | | | | | | |
| Yankee 1 | *Abies grandis*,<br>*Pseudotsuga menziesi* | *Pteridium aquilinum-Elymus glaucus*;<br>*Carex pensylvanica-Bromus* spp.[e];<br>*Rubus parviflorus* | 1555 | S | 48-75 | VFSL | 1942 | 68 / 6 |
| Yankee 2[f] | *Abies grandis*,<br>*Pseudotsuga menziesi* | *Pteridium aquilinum-Elymus glaucus*;<br>*Carex pensylvanica-Bromus* spp.;<br>*Rubus parviflorus* | 1555 | S | 48-75 | - | 1942 | 50 / 5 |
| Walker 1 | *Abies grandis* | *Pteridium aquilinum-Elymus glaucus*;<br>*Carex pensylvanica-Bromus* spp.;<br>*Rubus parviflorus* | 1497 | SE | 45 - 50 | SiL | 1942 | 113[g] / 10 |
| Walker 2 | *Abies grandis*,<br>*Pseudotsuga menziesii* | *Pteridium aquilinum-Elymus glaucus*;<br>*Carex pensylvanica-Bromus* spp<br>*Rubus parviflorus* | 1535 | SE | 20 - 56 | VFSL | 1942 | 151 / 6 |
| Ollalie | *Abies grandis*,<br>*Pinus contorta* | *Carex pensylvanica-Bromus* spp.-<br>*Haplopappus greenei* | 1520 | SSW | 12 - 21 | VFSL | 1918-1920[h] | 119 / 10 |
| Aspen 1 | *Abies lasiocarpa*,<br>*Picea engelmannii*,<br>*Tsuga mertensiana* | *Deschampsia caespitosa-Hypericum anagalloides-Muhlenbergia filiformis*;<br>*Carex sitchensis* | 1280 | NE | 0 - 17 | SiCL (H) | 1942 | 88 / 10 |
| Aspen 2 | *Abies lasiocarpa*,<br>*Picea engelmannii*,<br>*Tsuga mertensiana* | *Deschampsia caespitosa-Hypericum-anagalloides-Muhlenbergia filiformis*;<br>*Carex sitchensis* | 1283 | N | 0 - 8 | VFSL, SiC (H) | 1942 | 70 / 18 |
| Cow 1 | *Pinus contorta* | *Deschampsia caespitosa* | 1343 | flat | 0 | SL (H) | 1946 | 110 / 6 |
| Cow 2 | *Pinus contorta* | *Deschampsia caespitosa* | 1343 | flat | 0 | SL (H) | 1946 | 114 / 6 |
| **Subalpine sites** | | | | | | | | |
| Racetrack | *Tsuga mertensiana* | *Phyllodoce empetriformis-Cassiope mertensiana* | 1881 | NE | 0 - 50 | S, SL,VFSL | 1938 | 100 / 13 |
| Obsidian N[f] | *Tsuga mertensiana*,<br>*Abies lasiocarpa* | *Phyllodoce empetriformis-Cassiope mertensiana* | 1870 | NE | 41 | - | 1921 | 50 / 2 |
| Rebe | *Tsuga mertensiana*,<br>*Abies grandis*,<br>*Abies lasiocarpa* | *Festuca viridula* | 1598 | W | 21 - 30 | SiL | 1947 | 83 / 5 |
| James | *Tsuga mertensiana*,<br>*Abies lasiocarpa* | *Festuca viridula* | 1832 | SW | 15 - 27 | SL | 1938 | 98 / 11 |
| Obsidian S | *Tsuga mertensiana*,<br>*Pinus albicaulis* | *Festuca viridula* | 1869 | WSW | 10 - 15 | SL, FSL | 1921 | 60 / 19 |
| Twin | *Tsuga mertensiana* | *Festuca viridula* | 1830 | SSW | 0 - 22 | VFSL, SiL, S | 1938 | 90 / 30 |
| Lowder 1 | *Tsuga mertensiana*,<br>*Abies lasiocarpa* | *Arenaria capillaris* | 1668 | E | 0 - 17 | SiL | 1942 | 76 / 12 |
| Lowder 2 | *Tsuga mertensiana*,<br>*Abies lasiocarpa* | *Festuca viridula* | 1669 | NW | 0 - 2 | SiL | 1942 | 93 / 10 |

[a]From Halpern et al. (1984); [b]Soil texture codes: FSL = fine sandy loam, S = sand, SiC = silty clay, SiCL = silty clay loam, SL = sandy loam, SiL = silty loam, VFSL = very fine sandy loam; [c](H) = hydric soils; [d]Maximum transect width (see Methods); [e]*Bromus carinatus* and/or *B. sitchensis*; [f]Non-permanent transect established in 1993 (see Methods); [g]A 63-m long transect was established in 1983 and lengthened to 113 m in 1993; [h]Precise date of closure is unknown.

(basal or breast-height), and position along the transect were recorded for each individual.

All trees were aged by non-destructive means to permit future measurement. Three methods were used depending on the diameter and species. First, for trees with basal diameters > 6 cm, increment cores were extracted. Cores were taken as low to the ground as possible and coring height was recorded. Cores were mounted, sanded, and annual rings counted in the laboratory using a dissecting microscope. For samples that did not include the pith, the number of missing rings was derived from an estimate of the distance to pith divided by the average width of the inner 5 - 20 rings present in the core (Miller 1995). To obtain a final estimate of tree age, an estimate of age-to-coring-height was added based on regression equations developed from destructive sampling of small trees off the transects (Miller 1995).

Terminal bud scale scars were used to age trees with basal diameters < 6 cm. Because bud scale scars generally underestimate true age, species-specific regression equations were used to adjust these estimates (Miller 1995). Bud scale scars were counted only to the point where they were obscured by basal wounds, bark expansion, or ground-layer moss. As with cored trees, an estimate of age to the height of the last bud scar counted was added to the bud scar tally.

Finally, for small individuals of *Tsuga mertensiana* (which do not produce annual bud scale scars), ages were predicted from height or diameter. Regression equations were developed from destructive sampling of trees off the transects (range of $R^2$: 0.356 - 0.921; Miller 1995). Separate equations were constructed for each meadow in which *T. mertensiana* was abundant.

### *Data analysis*

We used Detrended Correspondence Analysis (Hill 1979; Gauch 1982) of the transect-level vegetation data in combination with the physical site descriptors to (1) portray major gradients in species composition among study sites, (2) infer the relative positions of sites and dominant species along gradients of physical environment, and (3) place patterns of tree establishment within the context of these gradients of environment and vegetation. Ordination was performed on composite samples representing the average cover of all species found in the meadow and ecotonal portions of each transect. Untransformed cover data were used and the standard set of defaults were implemented in the program DECORANA (Hill 1979).

For each transect, tree population age structures were developed to portray the temporal patterns of establishment at each site. Age structures for the ecotonal and meadow portions of each transect are expressed as the proportion of total establishment contained within each age class. Age-class widths (3 - 20 yr) increase with age to allow for the increasing likelihood of error in estimating the ages of older trees. Tree ages were also plotted as a function of distance along the transect to portray the spatial pattern and timing of establishment at each site.

To explore relationships between timing of establishment and climatic histories, tree densities per age class were correlated with seasonal climatic variables. For these analyses, we used the subset of trees from the ecotonal and meadow portions of each transect. Correlations were limited to the period of reliable weather records for the Cascade Range (1895-1993). Seasonal precipitation and temperature (Division 4, west-slope Cascades; Anon. 1990; Anon. 1991-1993) were averaged for the intervals defined by each age class at each site. Climatic seasons were defined as spring (March-May), summer (June-August), autumn (September-November), and winter (December-February). Historical data on the depth of snowpack in the study area are limited. We used the average depth of snowpack in early April at Three Creeks Meadow (1925 m a.s.l.) on the eastern boundary of TSBR (Oregon Climate Service database, Portland). In general, independent variables were normally distributed but establishment densities often were not. Thus, Pearson and Spearman rank correlation coefficients were calculated as appropriate (Zar 1984).

Weather data were supplemented with longer-term, but potentially less reliable instrumental and proxy records of climate. These included: (1) data on temperature and precipitation for Portland, Oregon (Anon. 1990; Anon. 1991-1993); (2) mean annual temperature at Longmire, Washington reconstructed from tree rings (Graumlich & Brubaker 1986); (3) depth of snowpack in mid-May at Paradise, Mount Rainier National Park, Washington (Paradise Ranger Station database); (4) hydrologic year (October to October) snowfall at Crater Lake National Park, Oregon (Anon. 1990); and (5) changes in mass of the Collier Glacier which flanks North and Middle Sister (McDonald 1995).

The historical grazing records for TSBR are incomplete, largely qualitative, and document areas larger than our individual study sites. Consequently, we focused on relationships between the *onset* of establishment and the closure of grazing allotments (ca. 1918-1947; Elliot 1946; Johnson 1985).

## Results

### *Gradients in vegetation and environment*

Site and species ordinations support our previous interpretations of vegetation-environment relationships in these meadows (Halpern et al. 1984). Meadow communities are arrayed across complex environmental gradients that incorporate variation in elevation, landform, topography, and hydrology (Fig. 2, Table 1). The primary gradient represented by Axis 1 separates hydric basins and poorly drained flats (dominated by *Carex sitchensis*,

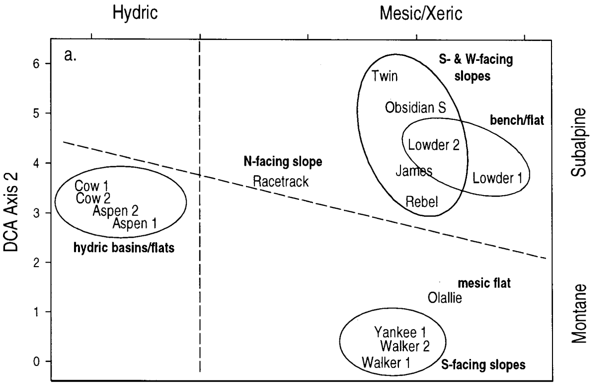

**Fig. 2.** Detrended Correspondence Analysis ordination of samples from 15 out of 17 transects (the two temporary transects, Obsidian N and Yankee 2, are not shown because specis compositioinal data were not collected). Sample scores are based on the average species composition of all 1 m × 1 m plots within the meadow and ecotonal portions of each transect.

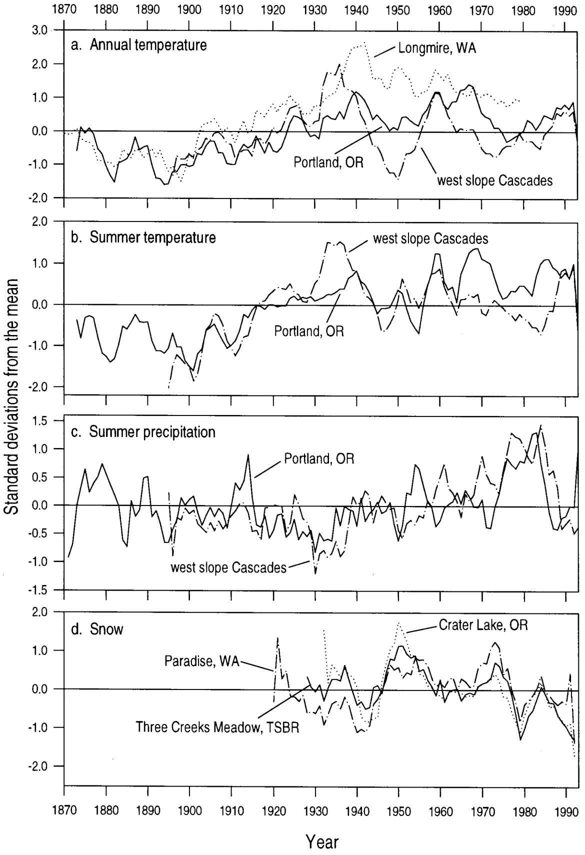

**Fig. 3.** Variation in selected climatic variables for the period 1870-1993 expressed as standard deviations from the mean. Data are 5-yr running means. **a.** Annual temperature for Portland, Oregon; west-slope Cascades; and Longmire, Washington. **b.** Summer (June-August) temperature for Portland, Oregon and west-slope Cascades. **c.** Summer precipitation (June-August) for Portland, Oregon, and west-slope Cascades. **d.** Depth of snowpack in mid-April at Three Creeks Meadow, Oregon (eastern edge of TSBR) and in mid-May at Paradise, Mount Rainier NP, Washington; and hydrologic year (October to October) snowfall at Crater Lake NP, Oregon. See Data analysis for sources.

*Deschampsia caespitosa* and *Vaccinium occidentale*) from more mesic and xeric communities. Along a secondary gradient lower-elevational, montane sites dominated by *Rubus parviflorus*, *Pteridium aquilinum*, *Bromus* spp. and *Carex pensylvanica* are separated from higher elevational, subalpine sites. The latter include north-facing slopes that support late snow-melt communities dominated by *Phyllodoce empetriformis*, *Cassiope mertensiana* or *Carex nigricans*, and south-facing slopes and flats dominated by *Festuca viridula*, *Lupinus latifolius* and *Polygonum newberryi*.

### *Temporal trends in climate*

Climate has changed markedly with time. Although individual climatic factors appear to have varied independently, a general pattern emerges. Mean annual and summer temperatures rose consistently from the turn of the century through ca. 1940 (Fig. 3a, b), while precipitation remained below average (Fig. 3c). Thus, the period between 1920 and 1945 was characterized by unusually warm and dry growing seasons. A warm, but wetter period followed (ca. 1945-1985), and more recently (through 1993) temperatures have been above average and precipitation below average. Trends in snowfall or snow accumulation have varied regionally, but values were generally below average for the periods 1920-1945 and 1975-1993 (Fig. 3d).

### *General patterns of tree invasion*

Tree invasion of meadows in TSBR has been widespread during the last century (Fig. 4). The composition, timing, and magnitude of establishment varied greatly among the sites sampled. In general, tree establishment has been less dense in montane (Fig. 4a-h) than in subalpine (Fig. 4i-p) meadows. Invasion into montane meadows has been dominated by *Abies grandis* on mesic hill-slopes and *Abies lasiocarpa*, *Picea engelmannii* and *Pinus contorta* in hydric basins. *Tsuga mertensiana* and *A. lasiocarpa* have been the principal invaders of subalpine meadows. Establishment began prior to 1900 at some sites (Fig. 4c, g), but most meadows have been invaded more recently, with peak establishment occurring mid-century (Fig. 4f, i, m) or later (Fig. 4c, g, h, j, n). At some sites, rates of establishment have increased gradually over time (Fig. 4j, n) while at others invasion has been more episodic, peaking at one or more times (Fig. 4c, f, l, m, p). The apparent high density of establishment at many sites during the period 1990-1993 may be a sampling artifact: trees 1 - 3 yr old at the time of census (1993) may have died subsequently because seedling mortality rates are typically high.

### *Tree invasion in the montane zone*

Meadows in the montane zone of the central Cascades are largely confined to three positions on the landscape: steep, south-facing slopes; small, hydric basins; and broad areas of flat and poorly drained topography (Fig. 2). Spatial and temporal patterns of establishment, as well as the factors associated with invasion, vary among these landforms.

On south-facing slopes (Yankee 1 and 2, Walker 1 and 2; Table 1), invasion was synchronous with changes in local disturbance regime and climate. For example, tree

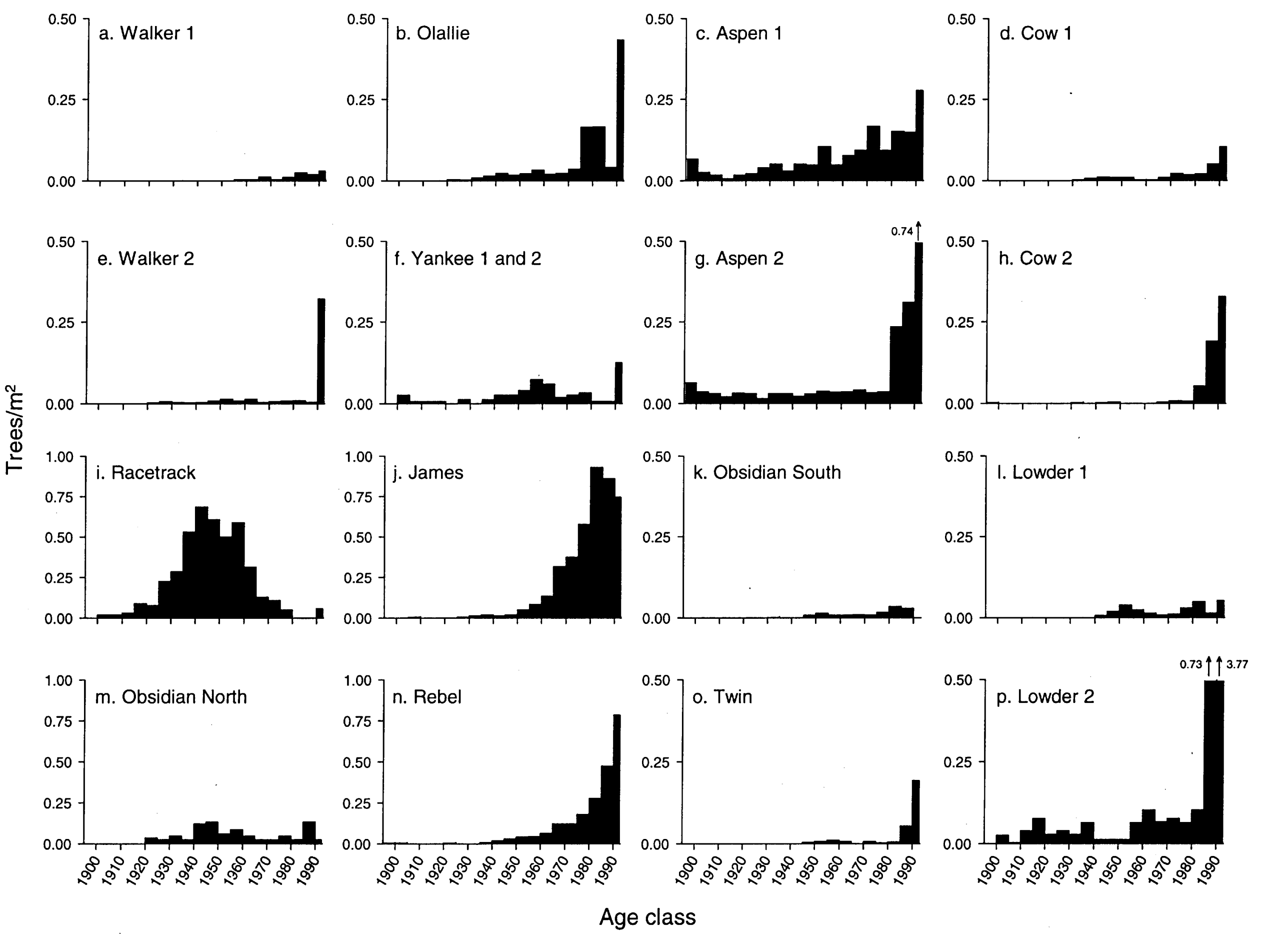

**Fig. 4.** Density of tree establishment (trees/m$^2$) by age class in the meadow and ecotonal portions of each transect for the period 1900-1993. **a-h.** Montane sites; **i-p.** Subalpine sites. Data for Yankee 1 and 2 are combined (the latter was established in 1993 to increase the sample size of trees). Note the variation in the scale of the Y axes.

establishment at Walker 1 increased soon after sheep were removed from these hill-slopes (ca. 1942, Fig. 5b) and with a return to cooler, wetter springs and summers (Fig. 3, Table 2). Establishment of the principal invader, *Abies grandis,* which characterizes the adjacent forest, was greater in upper-slope communities with shallow soils (dominated by *Carex pensylvanica-Bromus* spp. and *Pteridium aquilinum-Elymus glaucus*), than in more lush, lower-slope communities with deep loamy soils (dominated by *Rubus parviflorus*) (Fig. 5a).

At Ollalie Meadow (Table 1), spatial and temporal patterns of invasion are more complex but are closely linked with changes in grazing history (Fig. 6). Ollalie occupies a transitional area between the steep, highly dissected slopes of the Western Cascades and the gentle, rolling topography of the High Cascades. Sheep grazing initiated in 1872 (G.W. Williams pers. comm.) resulted in severe erosion, loss of vegetation, and eventual closure of the allotment ca. 1918 (Kuhns 1917). In addition, in 1910, the center of the meadow was fenced and packstock associated with a back-country guard station were allowed to graze until the station was abandoned in the late 1940s or early 1950s. There are three distinct bands of *Abies grandis* forest at Ollalie (Fig. 6a) with the oldest originating between 1860 and 1870, prior to the introduction of sheep (Fig. 6a). The second band of forest, situated closer to the current meadow, established soon after sheep were excluded (ca. 1918) (Fig. 6b). The third, which is more diverse in composition, initiated in 1950 in the formerly-fenced center of the meadow (Fig. 6c).

In hydric meadow basins in the montane zone, tree invasion is poorly correlated with most climatic factors and grazing histories. For example at Aspen 1 and 2 (Table 1), although establishment densities correlate with spring precipitation (Table 2), relatively continuous recruitment occurred, primarily of *Abies lasiocarpa* and *Picea engelmannii*, both uncommon in the surrounding

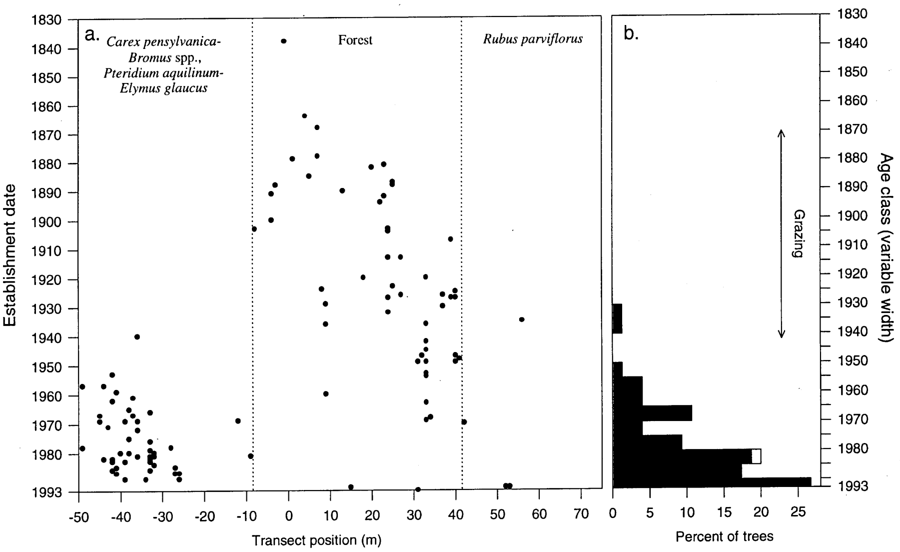

**Fig. 5.** Spatial and temporal patterns of tree establishment at Walker 1 (montane). **a.** Dates of establishment of all trees as a function of position along the transect. Vertical dotted lines define the boundaries between forest and meadow. Meadow occurs both upslope (negative distances) and downslope (positive distances) from a ca. 55 m-wide band of forest. **b.** Combined age structure of trees in both meadows expressed as the percentage of total establishment. Species are *Abies grandis* (solid circle/solid bar) and *Pseudotsuga menziesii* (open circle/open bar). Age-class widths vary (see Methods). The period of sheep grazing is defined by the two-ended arrow.

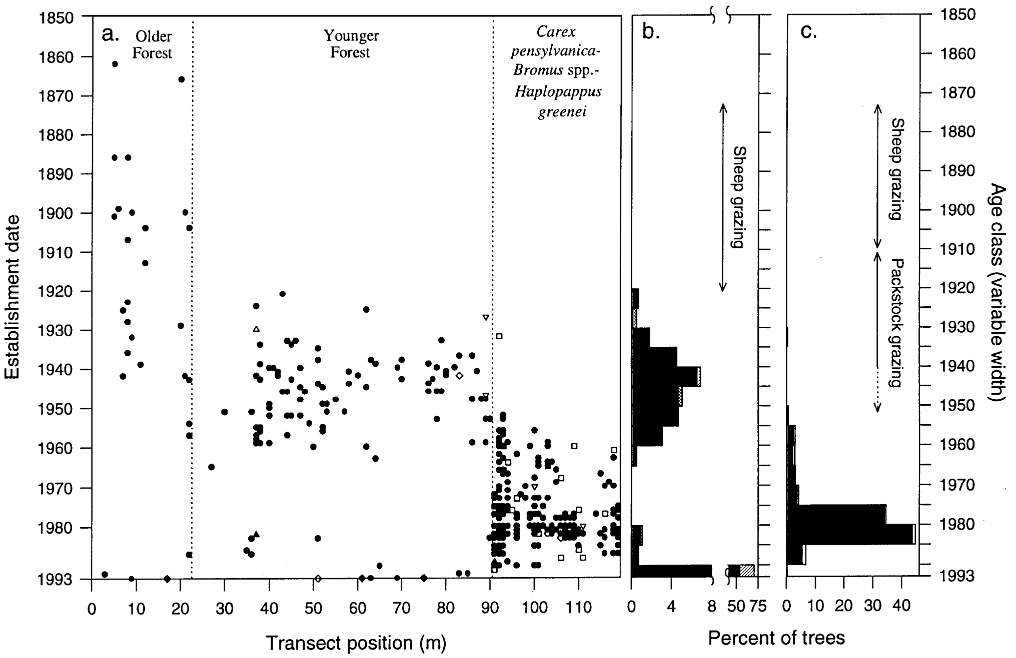

**Fig. 6.** Spatial and temporal patterns of tree establishment at Ollalie (montane). **a.** As in Fig. 5, vertical dotted lines define the boundaries between older forest, younger forest, and meadow. **b.** Age structures of trees in the younger forest (23-90 m) and **c.** in the meadow (90-119 m) expressed as the percentage of total establishment within each section of the transect. Species are *Abies grandis* (solid circle/solid bar), *A. lasiocarpa* (open triangle/horizontal cross-hatched bar), *Pinus contorta* (open square/open bar), *Picea engelmannii* (open circle/vertical-lined bar), *Pseudotsuga menziesii* (open diamond/rising right-lined bar), *Tsuga mertensiana* (solid triangle/rising left-lined bar), and all other species (open triangle down/diagonal cross-hatched bar).

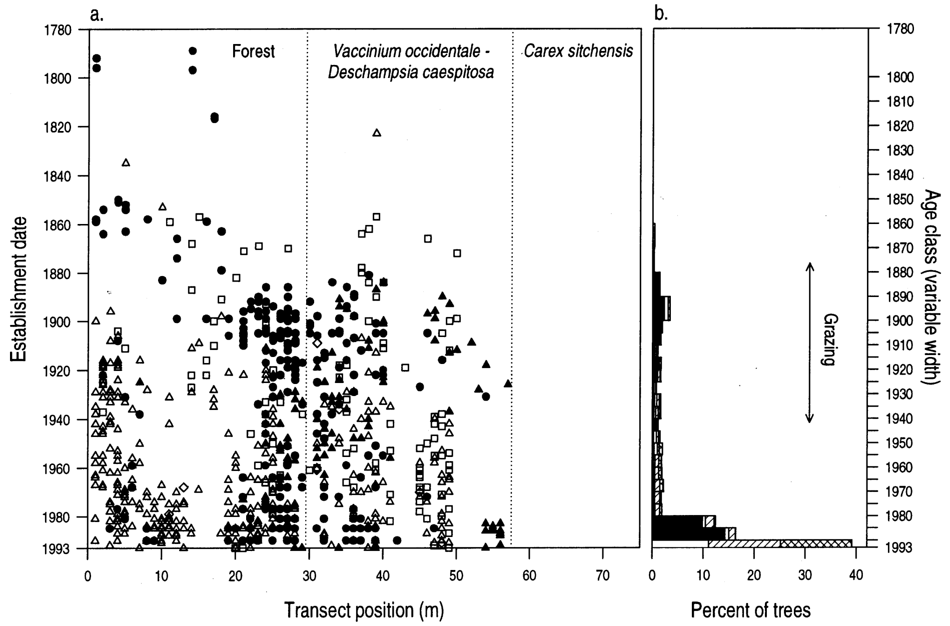

**Fig. 7.** Spatial and temporal patterns of tree establishment at Aspen 2 (montane). **a.** Dates of establishment of all trees as a function of position along the transect. Vertical dotted lines define the boundaries between forest, ecotone and meadow. **b.** The age structure of trees in the ecotone and meadow, expressed as the percentage of total establishment. Species are *Abies amabilis* (open triangle/ rising right-lined bar), *A. lasiocarpa* (open square/diagonal cross-hatched bar), *Picea engelmannii* (solid triangle/open bar), *Tsuga mertensiana* (solid circle/ solid bar), and all other species (open diamond / horizontal cross-hatched bar).

**Table 2.** Significant correlations between tree establishment (tree density per age class) and independent climatic variables for the 17 transects. Climatic seasons are spring: March-May, summer: June-August, autumn: September-November and winter: December-February. All correlations are positive.

| Transect | Climatic variable | Correlation coefficient Pearson | Spearman | *P* < |
|---|---|---|---|---|
| **Montane sites** | | | | |
| Yankee 1 | summer ppt. | | 0.59 | .010 |
| Yankee 2 | -* | | - | - |
| Walker 1 | spring ppt. | | 0.47 | 0.050 |
| | summer ppt. | | 0.49 | 0.050 |
| Walker 2 | spring ppt. | | 0.56 | 0.020 |
| | summer ppt. | | 0.52 | 0.050 |
| Ollalie | - | | - | - |
| Aspen 1 | spring ppt. | 0.68 | | 0.001 |
| Aspen 2 | spring ppt. | | 0.51 | 0.050 |
| Cow 1 | summer ppt. | | 0.71 | 0.001 |
| | spring ppt. | | 0.49 | 0.050 |
| Cow 2 | summer ppt. | | 0.51 | 0.050 |
| **Subalpine sites** | | | | |
| Racetrack | - | - | | - |
| Obsidian N | summer ppt. | 0.45 | | 0.050 |
| Rebel | summer ppt. | 0.48 | | 0.050 |
| | spring ppt. | 0.46 | | 0.050 |
| James | spring ppt. | | 0.45 | 0.050 |
| | summer ppt. | | 0.65 | 0.005 |
| Obsidian S | summer ppt. | | 0.63 | 0.005 |
| Twin | spring ppt. | | 0.62 | 0.005 |
| | summer ppt. | | 0.60 | 0.010 |
| Lowder 1 | summer ppt. | 0.81 | | 0.001 |
| | spring ppt. | 0.53 | | 0.020 |
| Lowder 2 | summer temp. | | 0.52 | 0.020 |

*Dashes indicate that no climatic variables were significantly correlated with establishment.

*Tsuga mertensiana* forest (Fig. 7a, b). Spatially, trees are clumped either beneath large, old (120+ yr) *A. lasiocarpa* or on drier microsites dominated by *Deschampsia caespitosa* or *Vaccinium occidentale*. Only in rare instances (i.e., during a series of exceptionally warm and dry summers ca. 1985-1990), did *Picea* establish in more hydric vegetation.

In contrast, tree invasion has been more episodic in hydric meadows that characterize the broad, flat, and poorly drained topography of the southwestern portion of TSBR. Along two widely separated transects in the *Deschampsia*-dominated communities of Cow Swamp (Cow 1 and 2; Table 1), *Pinus contorta* dominated the recruitment, although it was only a minor component of the surrounding *Picea engelmannii* forest (Fig. 8a). Establishment is highly clumped and individuals can be found > 100 m from the forest edge. Invasion began during the drought years of 1920-1945, long before sheep were excluded (1946; Fig. 8b). A second pulse of invasion began ca. 1965 coincident with relatively cool, wet weather, and establishment peaked between 1985 and 1993, a period characterized by some of the warmest and driest weather recorded.

### *Tree invasion in the subalpine zone*

Tree invasion of subalpine meadows has been widespread during the last century. For most sites (except Lowder Mountain, see below), the onset of establishment correlates with major changes in climate (Fig. 9a,

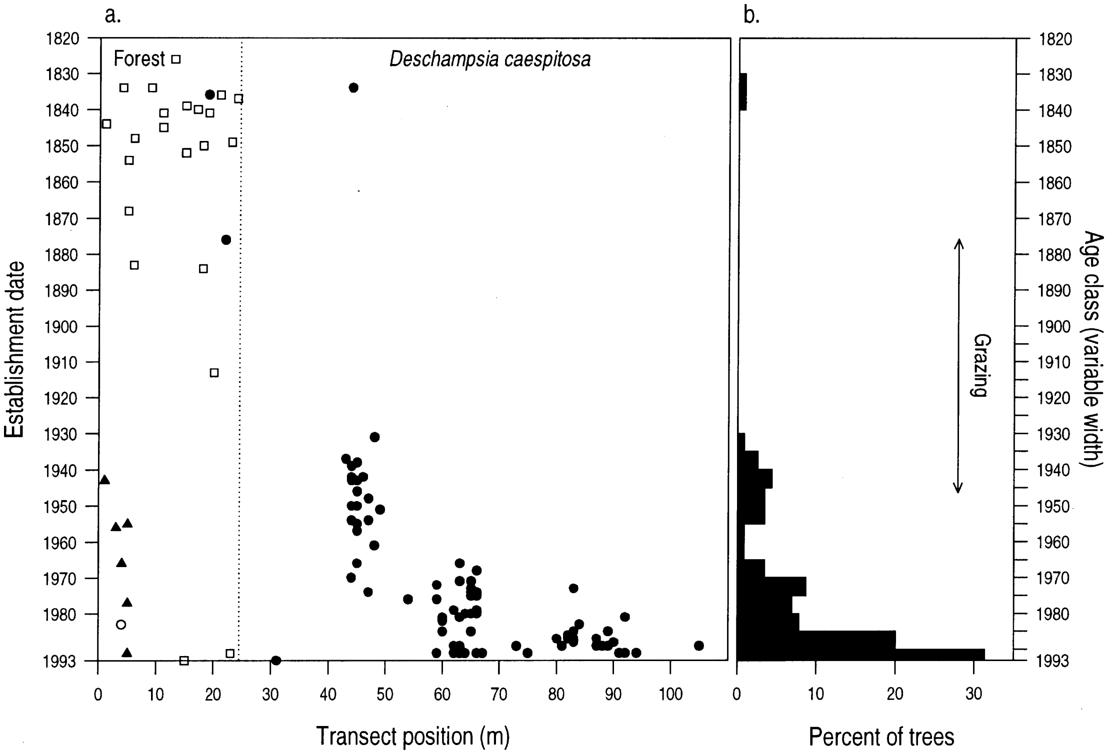

**Fig. 8.** Spatial and temporal patterns of tree establishment at Cow 1 (montane). Species are *Abies amabilis* (solid triangle), *Pinus contorta* (solid circle/solid bar), *Picea engelmannii* (open square/open bar), and *Tsuga mertensiana* (open circle). See Fig. 7 for other details.

b), but these dates differ markedly with aspect. To illustrate, we contrast patterns of invasion on north-facing slopes (Fig. 9c, d) with those on south- and west-facing slopes (Fig. 9e-h). The former are dominated by *Phyllodoce-Cassiope* heath-shrub at mid-slope positions and by *Carex nigricans* turf along lower slopes and flats (Racetrack, Obsidian N; Table 1, Fig. 10a). The latter are dominated by the perennial bunchgrass *Festuca viridula* (Rebel, James, Obsidian S, Twin; Table 1, Fig. 11a).

At Racetrack (north-facing), invasion of *Tsuga mertensiana*, concentrated in the heath-shrub portion of the meadow, began at the turn of the century (Figs. 9c and 10b), coincident with regional warming. Rates of recruitment accelerated between 1920 and 1945, concurrent with a period of regional drought (Fig. 9a, b). In contrast, few trees invaded south- or west-facing slopes before 1945 (Figs. 9e-h and 11b). Instead, *T. mertensiana*, *Abies lasiocarpa* and scattered *Pinus albicaulis* established later during a wetter period (Fig. 9a, b). Rates of establishment increased until 1985-1990, then declined at some sites with a return to drier conditions. Over the entire temporal record, establishment on south- and west-facing slopes was positively correlated with spring and summer precipitation (Table 2).

Correlations between the timing of tree establishment and cessation of grazing in the subalpine were generally poor, in contrast with upland montane sites. Two patterns are illustrative. First, at Racetrack, initial establishment (ca. 1920) began long before sheep were excluded (1938) (Fig. 9c). Second, despite widely varying dates of closure to sheep (1921-1947; Fig. 9e-h), the onset of establishment among south- and west-facing transects was relatively synchronous (ca. 1945).

Patterns of invasion on Lowder Mountain (Fig. 12) are an exception to the broader lack of correspondence with grazing history in the subalpine. This high plateau is contiguous with the east-west trending ridge system along which many of our south-facing montane meadows lie and grazing is known to have been intense (F.C. Hall pers. comm.). Marked differences in vegetation and ground surface features on Lowder suggest, however, that the severity of grazing disturbance varied across the plateau. To the south (Lowder 1), *Arenaria capillaris* dominates (Fig. 12a), soils are shallow, and cover of bare ground is high (ca. 50 %). Establishment of *Tsuga mertensiana* correlates with the removal of sheep in 1942 (Elliot 1946) (Fig. 12b); the oldest trees form a 10-m wide band parallel with the forest edge beneath which seedlings have continued to establish (Fig. 12a). In contrast, to the north (Lowder 2), the meadow is dominated by the bunchgrass, *Festuca*

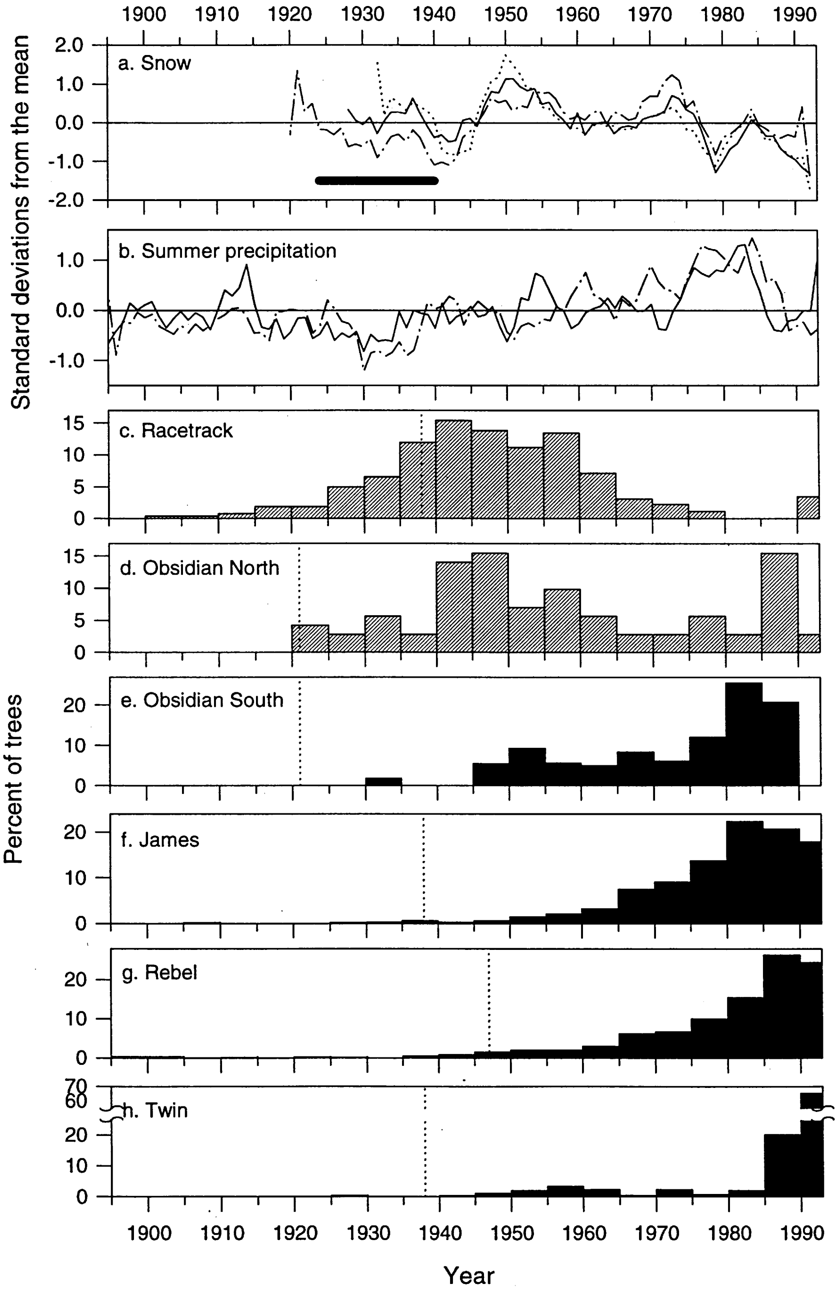

**Fig. 9.** Variation in climatic variables and tree establishment in subalpine meadows of TSBR. Climatic variables are 5-yr running means. **a.** Depth of snowpack in mid-April at Three Creeks Meadow, TSBR and in mid-May at Paradise, Mount Rainier NP, Washington; hydrologic year snowfall at Crater Lake NP, Oregon; and period of rapid retreat of the Collier Glacier, TSBR. See Data analysis for sources. **b.** Summer (June-August) precipitation for Portland, Oregon and west-slope Cascades. **c, d.** The age structures of trees in north-facing meadows; **e-h.** south- and west-facing meadows, expressed as the percentage of total establishment in each meadow. Vertical dotted lines represent dates of closure to sheep grazing. Note the variation in the scale of the Y axes.

*viridula* (Fig. 12c), and cover of bare ground is much lower (11%). Invasion of *T. mertensiana* has been relatively continuous during the century (Fig. 12d).

## Discussion

Recent tree invasion of meadows in the Three Sisters Wilderness Area/Biosphere Reserve has varied considerably in magnitude, spatial distribution, and timing. Since the turn of the century, establishment has been limited in some meadows and massive in others. At some sites, establishment has been episodic, correlated with changes in climate (e.g. temperature and/or precipitation), grazing pressure, or both; at other sites invasion has been continuous with time. Significant variation in patterns of establishment is not surprising given the diversity of microclimates, plant communities, and disturbance regimes. Although previous studies have concluded that recent invasion of mountain meadows in western North America has been a response to changes in climate (e.g. Brink 1959; Franklin et al. 1971; Lowery

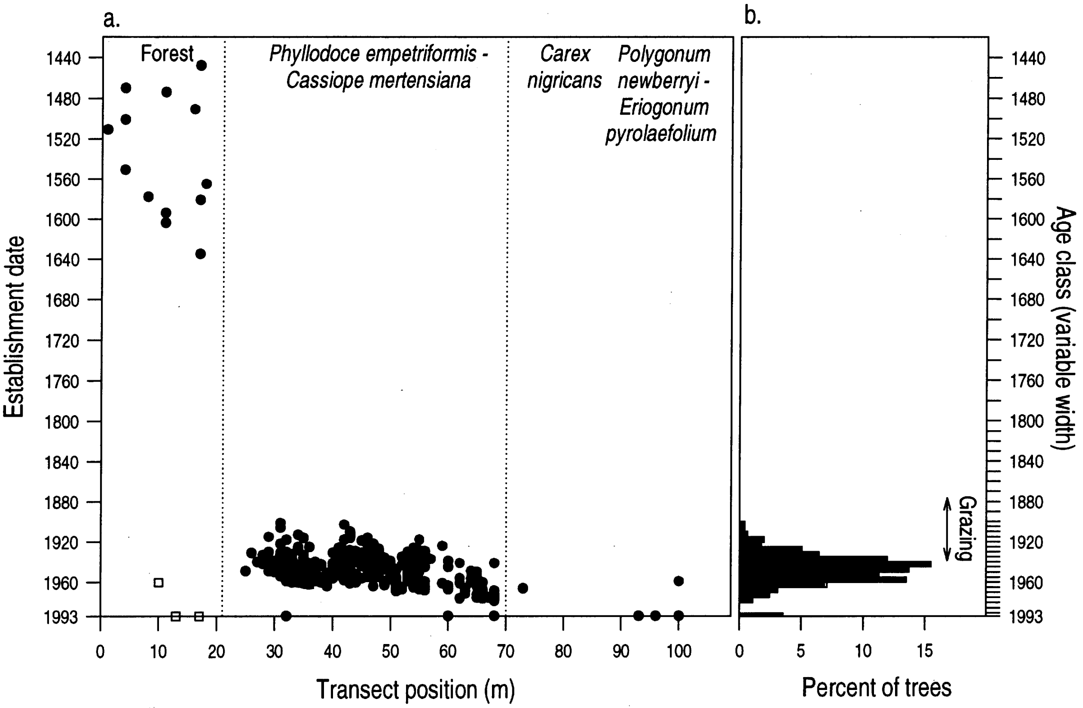

**Fig. 10.** Spatial and temporal patterns of tree establishment at Racetrack (subalpine). Species are *Abies amabilis* (open square/open bar) and *Tsuga mertensiana* (solid circle/solid bar). See Fig. 7 caption for other details.

1972; Kearney 1982; Heikkinen 1984a), disturbance by grazers (e.g. Dunwiddie 1977; Vankat & Major 1978; Vale 1981), or wildfire (e.g. DeBenedetti & Parsons 1979), our results suggest that the patterns and potential mechanisms of invasion are far more varied and complex.

The factors that shape tree establishment may be allogenic (e.g. climate change, grazing disturbance) or autogenic (e.g. microclimatic amelioration by established trees), although the precise nature of these controls and their relative importance vary in space and time. Where landform or topographic features impose immutable constraints on tree establishment, recruitment is restricted to those microsites in which environmental conditions are moderated (e.g. in hydric soils recruitment occurs on convexities). Where physical controls on establishment may vary temporally with changes in climate, recruitment is more likely to occur when environmental conditions become less harsh. Thus, on sites susceptible to heat stress or late-summer drought, tree establishment is triggered by cooler/wetter conditions. On sites in which growing seasons are short – limited by deep, persistent snow packs – establishment is induced by warmer and drier weather. Rochefort et al. (1994) have proposed a similar model of 'site amelioration' to describe the primary controls on subalpine tree establishment among broad climatic zones in western North America.

Our studies also suggest that once trees have established, autogenic factors may become increasingly important as individual trees or patches of trees alter the physical and/or biotic conditions that once inhibited establishment. As a consequence, rates of recruitment can accelerate with time and establishment may even continue during periods of unfavorable climate.

### *Methodological constraints and levels of uncertainty*

Our inferences about the causes of recent meadow invasion in TSBR are necessarily constrained by the retrospective and correlative nature of our approach. Therefore, we must temper our interpretations with the following caveats. First, grazing histories are often incomplete or largely qualitative, and encompass areas larger than the individual meadows of interest. Thus, the local intensity and duration of disturbance are difficult to quantify. Second, evidence of earlier establishment events may be erased by subsequent mortality; likewise, the occurrence and effects of low intensity fires are likely to go unrecorded. Third, the statistical significance of establishment-climate correlations can be biologically misleading because establishment events may not be independent (i.e. initial recruitment may facilitate subsequent establishment). Finally, the relatively short

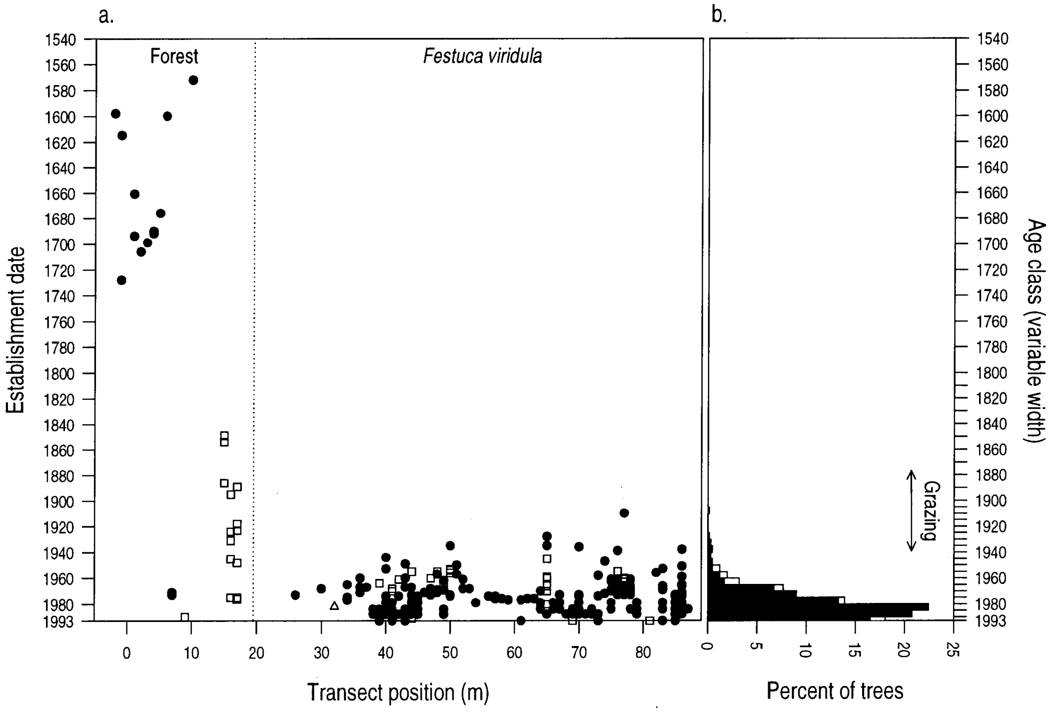

**Fig. 11.** Spatial and temporal patterns of tree establishment at James (subalpine). Species are *Abies lasiocarpa* (open square/open bar), *Pinus contorta* (open triangle/rising right-lined bar), and *Tsuga mertensiana* (solid circle/solid bar). See Fig. 7 for other details.

time period for which we have climatological data precludes consideration of longer-term trends and relationships. Given these constraints, we have emphasized the relationships between changes in climate or disturbance regime and the *onset* of invasion, and focus on the relatively recent period for which we have direct climatological and tree-age data. We cannot discuss the more distant aspects of meadow history, or ultimately, how or when they were created.

Although we cannot demonstrate causal relationships, our inferences about the factors that limit or trigger invasion, and how these vary over the landscape are strengthened by two general results. First, the patterns and correlates of invasion appear similar in sites of comparable physiography (elevation, aspect, topography) or vegetation, suggesting that the physical or biotic factors that promote or inhibit tree establishment operate over limited portions of the landscape. Second, where grazing disturbance is known to have been intense, the timing and spatial patterning of tree establishment are highly correlated with the removal of sheep. We discuss the nature of these relationships below, separating montane and subalpine sites for simplicity.

### *Patterns and correlates of invasion in the montane zone*

The patterns of invasion and the factors correlated with periods of recruitment appear to differ among the three primary meadow landforms of the montane zone. Hydric meadows appear to be among the most stable meadow types in this landscape. Geology and topography, through their effects on site hydrology (i.e. depth and stability of the water table) may limit the process of invasion. In small mountain basins where water tables remain high, forest-meadow boundaries are sharply defined and tree recruitment is restricted to 'tree islands' dominated by large, old colonists or to other elevated microsites. Consequently, these meadows are likely to remain open for centuries. Unless climatic conditions or basin hydrology change (e.g. Wood 1975; Benedict 1982), succession to forest will continue to be a slow process.

Where depth of the water table varies seasonally, as in the poorly-drained flats of the southern TSBR, recruitment has been more episodic. Yet causal relationships, if any, are difficult to infer. Grazing effects appear unlikely, as major establishment events either preceded or lagged behind the closure of grazing allotments. Climatic effects are possible, although patterns appear contradictory: establishment was positively associated with

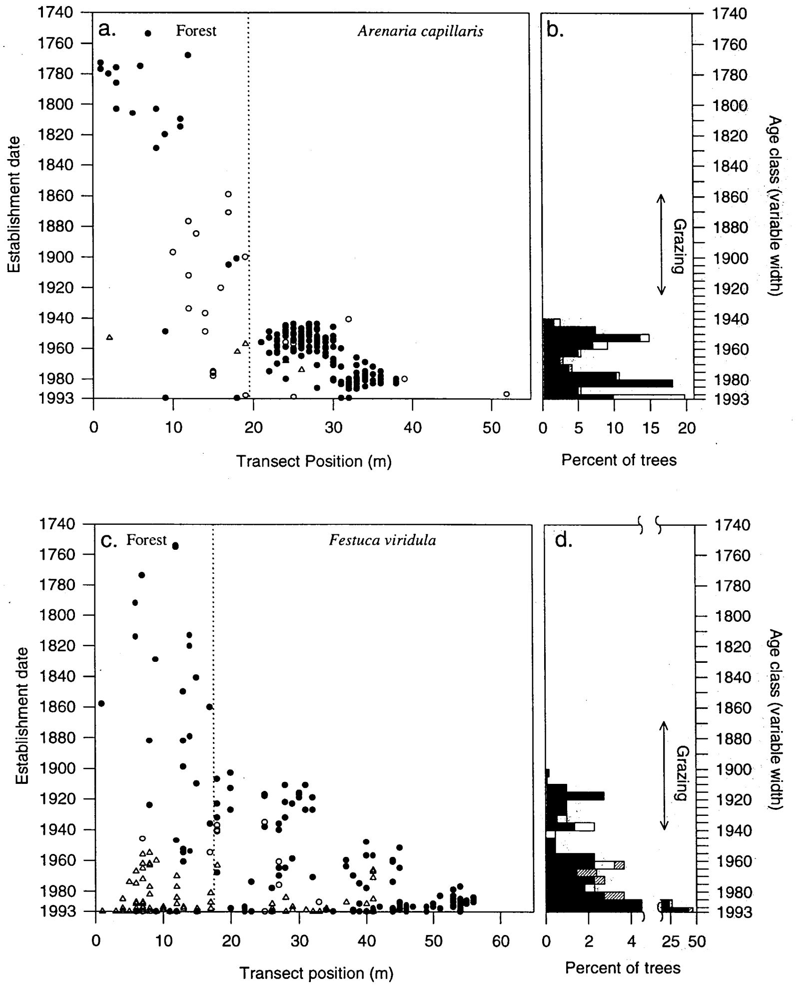

**Fig. 12.** Spatial and temporal patterns of tree establishment at **a, b.** Lowder 1 and **c, d.** Lowder 2 (subalpine). Species are *Abies amabilis* (open triangle/rising right-lined bar), *A. lasiocarpa* (open circle/open bar), and *Tsuga mertensiana* (sold circle/solid bar). See Fig. 7 for other details.

seasonal precipitation, but two of three distinct episodes of invasion coincided with drier periods. Potential relationships with climate may be difficult to detect because *Pinus contorta*, the primary invader in these meadows, tolerates a wide range of soil moisture conditions (Cochran 1972; Vankat & Major 1978; Ratliff 1985; Cunha 1992). That recruitment is clumped beneath large, older trees, suggests that, as in small hydric basins, invasion may be limited by high water tables and autogenic processes may be important in tree establishment. Large trees can facilitate establishment by creating raised microsites, reducing competition from ground-layer vegetation, or lowering the local water table through evapotranspiration (e.g. Kuramoto & Bliss 1970; Franklin et al. 1971; Magee & Antos 1992). Because of the patchy nature of establishment and the extremely large sizes of some of these meadow openings, succession to forest is likely to occur very slowly.

The factors leading to the invasion of upland meadows in the montane zone – those that typify relatively steep, south-facing slopes – are equally complex, although spatial and temporal patterns of establishment have been fairly consistent among the sites studied. The timing of establishment of *Abies grandis*, the principal invader, correlates both with changes in precipitation (a shift from drier to wetter conditions) and grazing regime. Thus, it is difficult to separate possible climatic effects from disturbance history. One or both factors may be important. For example, seedlings that establish on steep, south-facing slopes with shallow soils are exposed to summer drought or heat stress. High soil-surface temperature and/or low resulting soil moisture may induce mortality of newly established seedlings, preventing recruitment into open meadow vegetation (Baig 1972; Hickman 1976; Knapp & Smith 1982; Soll 1994; Rochefort & Peterson 1996). Cooler/wetter conditions may ameliorate this physical constraint.

The effects of a shift in climate may have been masked or magnified by the coincidental closure of grazing allotments in these upland sites. Large herbivores can directly inhibit tree seedling establishment by trampling or browsing (Ratliff 1985; Vallentine 1990), but once grazers are removed, the disturbed soils and vegetation that remain are often susceptible to tree invasion (Dunwiddie 1977; Vankat & Major 1978; Vale 1981; Ratliff 1985; Helms 1987; Taylor 1990; Vallentine 1990; Magee & Antos 1992). Spatial patterns of establishment on these sites – localized along upper slopes – lends support for a disturbance-mediated mechanism of invasion: upper-slope communities dominated by graminoids were preferred by grazing sheep and, thus, were more heavily disturbed than were lower slopes dominated by woody species (Kuhns 1917). On the other hand, poorer establishment of trees at lower-slope positions may reflect greater distances to seed sources or the competitive effects of a taller, denser shrub layer.

Trees that have established on these south-facing slopes exhibit rapid growth. Thus, as observed in other systems, the factors that maintain these meadow openings appear to limit tree establishment, but not growth (Franklin et al. 1971; Dunwiddie 1977). It is unclear what factors originally contributed to formation of these montane openings or to their long-term maintenance in an otherwise densely-forested landscape. Although empirical data on fire history are lacking for the area, catastrophic wildfire and/or periodic burning may have been important (e.g. Burke 1979; Vale 1981; Miller 1995). It is likely that fire suppression policies in the surrounding National Forest will encourage a more rapid succession to forest than might have occurred under the pre-settlement disturbance regime. At current rates of invasion, however, it may take several centuries for some of the larger meadows to close.

Where grazing by sheep (or packstock) in the montane zone is documented to have been especially intense, the effects of disturbance and subsequent release are strikingly apparent. Erosional gullies are still evident; meadow communities contain species characteristic of shallower, rockier, and more disturbed soils (including exotic taxa); and forest age structures and spatial distributions correspond closely with dates of release from anthropogenic influences. Prior to the introduction of sheep in these areas, it is likely that meadow openings were more common and larger than at present, possibly maintained by periodic wildfire. However, severe grazing disturbance followed by the complete removal of sheep has triggered a relatively rapid succession to forest.

### *Patterns and correlates of invasion in the subalpine zone*

Temporal patterns of invasion in the subalpine zone suggest strong climatic controls on tree establishment, but indicate a more complex dynamic than has been reported in earlier literature. Regional 20th century warming has often been cited as the trigger for recent invasion of subalpine meadows in the Pacific Northwest (Franklin et al. 1971; Heikkinen 1984a; Butler 1986; but see Rochefort et al. 1994; Woodward et al. 1995; Rochefort & Peterson 1996). Widespread tree establishment in the subalpine parkland of TSBR appears to have been triggered by a regional increase in temperature as well (ca. 1-1.5 °C since 1850; Burbank 1981, 1982; Graumlich & Brubaker 1986; Jones 1986). However, distinctly different temporal trends on north- and south-facing slopes suggests a strong interaction with patterns of precipitation.

The timing of invasion of north-facing slopes is consistent with the mechanism proposed for other subalpine sites in the Pacific Northwest: reduced precipitation results in lighter snowpacks, earlier snowmelt, longer growing seasons, and greater opportunities for establishment. Thus, during a shift to drier weather (1920 to 1945), *Tsuga mertensiana* abundantly invaded north-facing slopes, establishing primarily in communities dominated by *Phyllodoce empetriformis* and *Cassiope mertensiana*. Localized establishment in subalpine heather has been observed throughout the Northwest and has been attributed to the characteristic occurrence of heather on microtopographic convexities (thus, earlier release from snowpacks), to moderation of summer temperature and moisture stress by the evergreen foliage and woody stems of heather, and to greater retention of dispersed seed by the relatively dense vegetation (Brink 1959; Fonda & Bliss 1969; Arno 1970; Brooke et al. 1970; Kuramoto & Bliss 1970; Baig 1972; Douglas 1972; Rochefort & Peterson 1996).

In contrast with north-facing slopes, south-facing slopes in the subalpine area are snow-free earlier in the year, but are more susceptible to late summer drought. Predictably, recruitment was poor during drier periods, but increased during the wetter summers that followed. Establishment densities consistently correlate with high spring and summer precipitation suggesting that on south-facing slopes, ground surface temperatures and available soil moisture may limit the survival of germinants during years with low winter snowpack or early snowmelt. It is not surprising that the factors that appear to limit or promote invasion differ with aspect. At these elevations, subtle changes in topography can induce marked changes in local environment (e.g. snow accumulation, timing of snowmelt, and availability of soil moisture late in the growing season; Van Vechten 1960; Brooke et al. 1970; Kuramoto & Bliss 1970, Douglas 1972; Campbell 1973; Henderson 1973; Evans & Fonda 1990). Similar contrasts have been observed during the regeneration of subalpine forests after wildfire (Agee & Smith 1984) and in subalpine parklands of the Olympic Mountains (Woodard et al. 1995), Mt. Rainier (Rochefort

& Peterson 1996), and Mt. Lassen (northern California) (Taylor 1995).

In addition to climatic influences, our studies suggest that autogenic factors may further mediate tree establishment in the subalpine zone. Although warmer, drier weather may have triggered the initial invasion of north-facing meadows, subsequent establishment during cooler, wetter years may have been possible through the ameliorating influence of 'parent' trees. The boles and canopies of these larger trees may modify the microclimate by reducing or redistributing snowloads, by reradiating solar energy to create snowmelt craters, or by reduced scouring of seedlings by creeping or windblown snow and ice (Brooke et al. 1970; Lowery 1972; Heikkinen 1984b). A similar system 'inertia'has been proposed to explain the longer-term expansion of *T. mertensiana* in near-treeline environments (Taylor 1995).

Our studies offer limited evidence that historical changes in grazing regime have shaped recent invasion of subalpine meadows. It may be that grazing-associated disturbance was not sufficient to affect local vegetation or soils, or that effects on tree establishment were masked by those of a shifting climate. The strongest support for the absence of grazing-induced changes comes from establishment trends on south-facing slopes. Here, despite widely varying dates of closure to sheep, tree invasion remained relatively synchronous among transects and was closely timed to the onset of wetter weather. Moreover, *Festuca viridula* remains dominant in these subalpine meadows, suggesting that range deterioration was limited. However, where grazing was known to have been locally intense, indicators of severe disturbance persist, including extensive areas of bare ground, abundant gopher activity, and a unique ground-layer vegetation (Jardine & Anderson 1919; Moore & Reid 1951; Halpern et al. 1984). Similar to the pattern observed in intensively grazed montane meadows, trees established soon after sheep were removed.

Our reconstructions of the recent histories of invasion in these montane and subalpine systems suggest that their future dynamics will be driven by the interplay of regional changes in climate (Rochefort et al. 1994), attendant changes in disturbance regime (Franklin et al. 1991), and the continued expression of autogenic processes already in place. By considering an array of environmental conditions, meadow communities, and disturbance histories, we have provided evidence that the resulting patterns of change are likely to be complex, as the strengths of these effects can vary with site environment, vegetation, or time.

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